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Characterizing Movement Patterns and Spatio-temporal Use of Under-road Tunnels by Long-toed Salamanders in Waterton Lakes National Park, Canada

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Linnet Lake (Waterton Lakes National Park, Alberta) is the breeding site of a population of Long-toed Salamanders (*Ambystoma macrodactylum*) that has decreased dramatically over the last 15 years, partially due to vehicle-caused mortality occurring on an adjacent road. In May 2008, Parks Canada installed four amphibian tunnels under this road. We installed drift fences to direct salamanders toward tunnel entrances and monitored tunnel use with pitfall traps in 2008 and 2009. We used logistic regressions and Akaike's Information Criterion (AIC) to determine if probability of tunnel use differed among individual salamanders. Salamander road mortality decreased from 10% of the population to <2% following installation of tunnels and fences. In 2009, 104 salamanders were documented using tunnels. Salamanders were 20 times more likely to use tunnels when traveling to the breeding site than when leaving the site. Distance from tunnel entrances, sex, and body size did not have significant effects on tunnel use by salamanders. Although salamander movement was positively correlated with occurrence of precipitation, this relationship was much stronger when salamanders were leaving the breeding site. Variation in use between the four tunnels was positively correlated with soil moisture of surrounding habitat. Continued monitoring will be needed to determine if tunnel use by Long-toed Salamanders increases through time, and if decreased road mortality translates into population gains.

CONSTRUCTION of roads can drastically change natural landscapes by creating barriers to animal movement that consequently reduce population connectivity (Ascensão and Mira, 2007). Roads also promote animal–vehicle collisions, which is the leading human-induced source of direct mortality in terrestrial vertebrates (Forman and Alexander, 1998) and the greatest non-natural source of vertebrate death in protected areas, such as parks and reserves (Bernardino and Dalrymple, 1992; Kline and Svann, 1998). For temperate pond-breeding amphibians, vulnerability to road mortality can be high because their life histories often involve mass movements between aquatic breeding habitat and terrestrial habitats (see Andrews et al., 2008 for a review of effects of roads on amphibians and reptiles). They are also inconspicuous and slow moving, which increases their susceptibility and exposure to vehicles. For example, Clevenger et al. (2001) documented the movement of Tiger Salamanders (*Ambystoma mavortium*) across the Trans-Canada highway in Kananaskis, Alberta, and found 180 road-killed individuals along a 1 km stretch of road over a five-day migration period.

One conservation strategy used to minimize the negative effects of roads on wildlife is the installation of wildlife crossing structures, such as overpasses and tunnels, which are designed to improve road permeability to animal movements. The inclusion of wildlife crossing structures in the design and construction of roads is becoming increasingly common (Clevenger and Waltho, 2000). However, relatively few studies have examined the efficacy of these structures, and for those that have, success is variable (Brehm, 1989; Jackson and Tyning, 1989; Veenbaas and Brandjes, 1999; Allaback and Laabs, 2003; Mata et al., 2003; Lesbarrères et al., 2004). In 1987, two tunnels with associated drift fences were installed in Amherst, Massachusetts, to facilitate breeding migrations of Spotted Salamanders (*Ambystoma maculatum*; Jackson and Tyning, 1989). A mark–recapture study revealed that 68% of salamanders captured along the length of the drift fence and 76% of those observed at the tunnel entrance successfully passed through tunnels. These passages were deemed successful in reducing road mortality of Spotted Salamanders and maintaining migration corridors. In 1999, six tunnels were installed in an effort to protect the endangered Santa Cruz Long-toed Salamander (*A. macrodactylum croceum*) in Aptos, California (Allaback and Laabs, 2003). In 2000–2001, only 9% of the Santa Cruz Long-toed Salamanders that encountered drift fence passed through the tunnels.

The Long-toed Salamander (*Ambystoma macrodactylum*) is a species of mole salamander that occurs in a variety of habitats in the northwestern United States and adjacent Canada. In Alberta, the Long-toed Salamander has a limited range along the east slopes of the Rocky Mountains and is legally designated a ''species of special concern'' (Government of Alberta, 2009). Adult and juvenile Long-toed Salamanders spend the vast majority of their time in terrestrial habitats, overwintering in abandoned mammal burrows (Sheppard, 1977). As with other ambystomids (such as the Spotted Salamander; Douglas and Monroe, 1981), adult Long-toed Salamanders may migrate to and from breeding sites in the spring, during the fall, or they may split their migration between the two seasons. The majority of adult Long-toed Salamanders immigrate to breeding sites (wetlands and small lakes) shortly after spring melt and emigrate back to overwintering sites in summer or fall (Anderson, 1967). Young-of-the-year disperse throughout the terrestrial landscape in search of overwintering sites in the fall following metamorphosis (Beneski et al., 1986). Adult migration and juvenile dispersal usually take place nocturnally, primarily during or after precipitation (Fukumoto, 1995).

Linnet Lake, located in Waterton Lakes National Park (WLNP), is the breeding site of a population of Long-toed Salamanders that has recently undergone significant declines. In 1994, Fukumoto (1995) conducted a mark–recapture study

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by capturing salamanders along the roadside, and estimated the population to be 3856 (95% CI: 3274–4690) breeding adults. A subsequent mark–recapture study conducted in 2009 suggested that the salamander population had declined by about 65% over the last 15 years (Pagnucco, 2010). Park biologists largely attributed this decrease to mortalities on the Entrance Road, which separates salamanders breeding in Linnet Lake from terrestrial overwintering habitat to the west (Pearson, 2002). In May 2008, Parks Canada installed four concrete amphibian tunnels under the Entrance Road to reduce vehicle-caused mortalities of migrating Long-toed Salamanders and improve habitat connectivity (Smith et al., 2010).

Our primary research objectives were to: quantify the extent that road tunnels, and associated drift fences, reduced vehicle-caused mortality of Long-toed Salamanders; derive empirically based models predicting the probability of use of tunnels by individual Long-toed Salamanders; and determine the extent to which immigration and emigration are influenced by the occurrence of precipitation. Preliminary analyses showed appreciable variance in the use of the four tunnels by Long-toed Salamanders that likely reflected variance in habitat characteristics of the area adjacent to each tunnel. Thus, a secondary objective was to explain variance in use of the four tunnels by Long-toed Salamanders based on habitat characteristics.

We predicted that the installation of road tunnels would result in reduced levels of vehicle-caused mortality in 2008 and 2009 compared to levels observed in 1994 prior to the establishment of tunnels and arrays of directional fencing. We predicted that larger salamanders would be more likely to use tunnels than smaller salamanders. As terrestrial salamanders are vulnerable to desiccation (Feder, 1983) and resistance to desiccation is positively correlated with size (Ray, 1958), larger salamanders should be more tolerant of moving along a cement tunnel, which represents a 12 m stretch of dry, non-vegetated habitat. We predicted that capture rates of salamanders would be strongly and positively related to precipitation, which is true for other ambystomids, such as Small-mouthed (*Ambystoma texanum*) and Eastern Tiger Salamanders (*A. tigrinum tigrinum*; Williams et al., 2009). Given that previous studies on habitat selection of other ambystomid salamanders have identified soil moisture and canopy cover as important habitat variables for salamander use (deMaynadier and Hunter, 1998; Jenkins et al., 2006), we predicted that salamander capture rates would be higher in habitats with high soil moisture and extensive tree canopy. Determining how precipitation and habitat variables contribute to the temporal and spatial variation in salamander movement patterns will allow optimization of monitoring efforts in Waterton Park and at future sites of amphibian crossing structure installation, as well as inform the placement of these structures.

MATERIALS AND METHODS

Study site.—Linnet Lake (49°03′41″N, 113°54′18″W) in Waterton Lakes National Park is a small (3.5 ha), shallow (max depth = 5 m) water body situated adjacent to Middle Waterton Lake. Aspen (*Populus tremuloides*) and various conifers, including Lodgepole Pine (*Pinus contorta*) and White Spruce (*Picea glauca*), dominate the forest that immediately surrounds the lake. However, portions of the slope to the west of Linnet Lake are open and covered with grass.

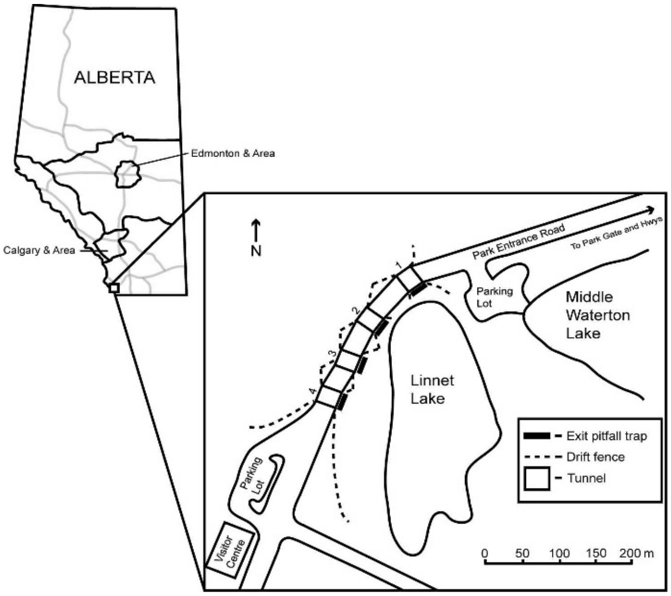

Fig. 1. Map of Linnet Lake area in Waterton Lakes National Park, Alberta, including locations of under-road tunnels, exit pitfall traps, and drift fences in 2009. Adapted from Fukumoto (1995).

Four amphibian tunnels were installed under the Entrance Road that runs parallel to Linnet Lake from 26 May to 4 June 2008 (Smith et al., 2010; Fig. 1). Each tunnel is a ''box culvert'' 60 cm wide by 52 cm high (AT500 Amphibian Tunnels, ACO Technologies, Shefford, UK). Each concrete section has slots along the top that allow air, moisture, and light into the tunnel. Segments were placed end to end to span the width of the road and the sidewalk that runs along one roadside. Tunnels are approximately 12 m in length and are 80–110 m apart.

Historical data.—In 1993–1994, Fukumoto (1995) conducted a study of the newly discovered population of Long-toed Salamanders breeding at Linnet Lake as part of a Master's thesis. The 1994 study includes large amounts of raw data that were used to describe the conditions of this salamander population in 1994. Surveys conducted in 1993 began long after the peak of the spring salamander migration, and as such, only data collected during 1994 were used as a basis of comparison for the effectiveness of the fence/tunnel system employed in 2008–2009. Additional pre-treatment data collected from other years would have been valuable, but were not collected.

Road mortality of Long-Toed Salamanders was estimated using night surveys in 1994. During surveys, an observer walked 500 m along the Entrance Road, paralleling Linnet Lake, and identified each amphibian encountered, alive or dead.

Breeding activity of Long-Toed Salamanders was first monitored at Linnet Lake in 1994 using night searches (Fukumoto, 1995). Night searches were conducted from 12 April–15 September 1994 along the 500 m section of the Entrance Road that parallels Linnet Lake which covered the entire migration corridor. Adults were marked by using unique toe-clips, and the Schumacher-Eschmeyer method was used to estimate the breeding adult population size in 1994.

Monitoring road mortality.—We estimated levels of road mortality by conducting visual surveys from 14 April to 14 October 2008 and from 2 May to 20 June 2009 daily before dawn, following the installation of drift fences (see below). During 2008 and 2009, the same procedures were employed along the same section of road as in 1994. Annual road mortality rates for each year were calculated as the number of Long-toed Salamanders found killed along the Entrance Road divided by the total number of salamanders captured alive on the road or in roadside traps.

Monitoring movement and tunnel use.—To collect data on Long-toed Salamander movements, we installed a drift fence and pitfall trap array system to intercept animals immigrating to Linnet Lake from terrestrial habitats and emigrating from Linnet Lake to terrestrial habitats. In April 2008, six weeks prior to the installation of tunnels, we installed continuous drift fencing on both sides of the same 500 m section of the Entrance Road that parallels Linnet Lake. Ends of drift fences were curved inward in an effort to reduce the possibility of salamanders circumventing the fences. Drift fencing was accompanied by pitfall traps that were installed at 18 m intervals along each fence, for a total of 44 pitfall traps (Pagnucco, 2010). Traps were checked daily between 0600–1000 hr from 14 April to 14 October. No young-of-the-year, only one juvenile, and 31 adult Long-toed Salamanders were captured from 1 September to 14 October 2008. Because of low sample sizes, we decided not to monitor the fall migration in 2009.

In an effort to bolster tunnel use by Long-toed Salamanders, we installed continuous directional fencing angled toward tunnel entrances in 2009, which has been suggested as a method to increase amphibian tunnel use (Jackson, 2003; Fig. 1). Total lengths of drift fences leading to each tunnel were 133 m (Tunnel 1), 159 m (Tunnel 2), 222 m (Tunnel 3), and 274 m (Tunnel 4). In 2009, we conducted fence surveys to monitor salamander movement instead of relying on pitfall traps along fences which captured salamanders moving along fences before they reached tunnel entrances. We collected salamanders during nightly searches from 3 May to 16 June by patrolling fences, beginning at 2200 hr each night (i.e., at sunset) and continuing for 30 min to 4 hr. During searches, we walked along each fence once, measuring and marking every salamander found, as detailed below. We marked the location of capture with the individual's identification number (see below) so we could determine initial distance from the nearest tunnel entrance.

In order to monitor tunnel use by Long-toed Salamanders in 2009, we installed a rectangular pitfall trap (76 cm in length, 20 cm in width, and 18 cm in depth) at the ''exit'' of each tunnel based on the dominant direction of salamander movement. From 22 April to 19 May, exit traps were located on the east side of the road to catch individuals immigrating to Linnet Lake to breed. Between 20 May and 19 August, traps were moved across the road to catch salamanders emigrating west from Linnet Lake back to terrestrial habitats (determined by nightly searches along the fences). In an effort to reduce predation and escape of amphibians, we placed a wooden cover over the pitfall traps (76 cm in length, 20 cm in width, and 20 cm in height). These rectangular pitfall trap covers were open only on the side facing tunnel exits, which minimized capture of animals that were not exiting tunnels. Traps were checked daily between 0600–1000 hr. We calculated ''fence/tunnel efficiency,'' defined as the percentage of animals encountering the fence that eventually passed through the tunnels (Jackson and Tyning, 1989) based on capture in exit pitfall traps.

In both years, we determined the sex and snout–vent length (SVL; mm) of each captured salamander. Using a ruler, SVL was measured as the distance from the tip of the snout to the terminal end of the cloacal vent. Sex was assigned based on body shape and morphology of the vent area (Fukumoto, 1995). We used a visible implant elastomer (VIE; Northwest Marine, Shaw, WA) to mark every captured salamander. We recorded the trap number and Julian date of capture for each salamander prior to releasing it on the opposite side of the road under cover, in the direction that it was headed.

Precipitation and habitat characteristics.—Daily precipitation totals were recorded at the Waterton Park Gate weather station (7 km from Linnet Lake). We measured three categories of habitat variables at locations every 15 m along each road fence from 22 to 30 May 2009: canopy cover (%), soil moisture content, and leaf litter depth (mm). Four estimates of canopy cover were made with a densiometer by facing each of the four cardinal directions, and then values were averaged. Due to disturbance caused by installing pitfall traps and fences, measurements of soil moisture and leaf litter depth were taken in an area 2 m perpendicular from the fence. We measured soil moisture content using a Kelway soil pH and moisture meter (% saturation) at each tunnel entrance, and averaged the two readings to produce one value per tunnel. Leaf litter depth (± 1 mm) was measured by inserting a ruler through the leaf litter and humus layer (i.e., the O soil horizon) until it came in contact with the A soil horizon (Crawford and Semlitsch, 2008).

Statistical analyses.—We used a chi-square test to determine if the proportion of Long-toed Salamanders captured in exit traps differed among the four tunnels. We used Akaike's Information Criteria (AIC) and the information-theoretic approach (Burnham and Anderson, 1998) to identify hypotheses regarding factors important in determining tunnel use by individual Long-toed Salamanders. Models included various combinations of the following parameters: body size, sex, distance (of encounter from nearest tunnel entrance), direction (immigrating or emigrating), as well as the interaction between distance and direction. Based on *a priori* predictions, we evaluated nine potential models using logistic regressions. Models with Δ_i $\mathrm{AIC_c} < 2$ were considered supported, and Akaike weights (w) were used to rank variable importance and adjust coefficients and odds ratios (Burnham and Anderson, 1998).

We identified peak adult immigration and emigration periods in 2008 and 2009 based on the dates that encompassed the 5th and 95th percentile of total captures (Paton and Crouch, 2002). Julian date of capture was converted to day of capture, with the first day of capture being coded as 1 within each breeding year (4 May 2008, 3 May 2009). We tested for differences in Long-toed Salamander capture rates (captures/day) between migration directions (immigration and emigration) and among years (1994, 2008, and 2009) on days with or without precipitation, as well as the interactions between these factors, with the G-test of independence (Sokal and Rohlf, 1981).

We used a multivariate analysis of variance (MANOVA) to determine how habitat characteristics (leaf litter depth, canopy cover, and soil moisture) differed among the four tunnels, using habitat data that were collected along fence sections in 2009. To meet the assumptions of parametric tests, canopy cover data were arcsine square-root transformed prior to analyses (Zar, 1999). Tukey's HSD was used to determine differences between pairs of means. All statistical tests were conducted with SPSS v.16 (SPSS Inc., Chicago, IL; http://www-01.ibm.com/software/analytics/spss/). Akaike's Information Criterion values were obtained using formulas from Burnham and Anderson (1998) in Excel 2007 (Microsoft, Redmond, WA).

RESULTS

Road mortalities.—In 2008, we found six live amphibians (five Long-toed Salamanders, one Western Toad [*Anaxyrus boreas*]), 16 road-killed amphibians (ten Long-toed Salamanders, six Western Toads), and two road-killed Wandering Garter Snakes (*Thamnophis elegans vagrans*) along the Entrance Road. Seven of the road-killed Long-toed Salamanders were found during the spring migration period (4 May–10 June 2008) prior to tunnel installation, and three during the fall period (3 September–14 October 2008). In 2009, we found two road-killed Long-toed Salamanders, both in early May. The percentage of road-killed adult Long-toed Salamanders (calculated as the number of road-killed individuals divided by the total number of salamanders migrating across the road) was 1.6% in 2008 and 0.6% in 2009. By contrast, road-killed Long-toed Salamanders represented 10% of Long-toed Salamanders (67 of 690) migrating across the Entrance Road in 1994 (Fukumoto, 1995), when drift fences and tunnels were absent. Fences installed in 2008–2009 had the potential to concentrate salamander movement, resulting in a larger proportion of the salamander population being observed in 2008–2009 than in 1994. However, the roadside is rocky with sparse vegetation, thus the probability of detection of salamanders should have been equally high in the 1994 and 2008–2009 studies, making these two estimates of road mortality comparable.

Tunnel use by Long-toed Salamanders.—In 2009, a total of 104 adult Long-toed Salamanders were captured in exit traps, presumably after successfully moving through the tunnels, 74% of which were captured immigrating to Linnet Lake. Of the 91 Long-toed Salamanders captured along the fence during night surveys during the 13-day peak immigration period, 21 were later captured in ''exit'' traps after using tunnels, resulting in a fence/tunnel efficiency rating of 23%. During the 23-day peak emigration period, two of 179 salamanders caught along fences were caught in tunnel ''exit'' traps, for a fence/tunnel efficiency rating of 1%. Four Gray Tiger Salamanders (*Ambystoma mavortium*) and seven Western Toads were also captured in exit traps. Tunnels were not equally used by Long-toed Salamanders ($\chi^2 = 38.0$, df = 3, $P < 0.001$). Of the 104 Long-toed Salamanders captured exiting tunnels, almost half were caught at Tunnel 3 (49%), compared to Tunnel 1 (7%), 2 (26%), and 4 (18%). This pattern of differential use is retained even when total exit trap captures were corrected for total length of drift fences leading to each tunnel: Long-toed Salamanders captured per meter fencing = 0.05 (Tunnel 1), 0.17 (Tunnel 2), 0.23 (Tunnel 3), and 0.07 (Tunnel 4). On average, Long-toed Salamanders spent 3.5 ± 0.1 nights moving along fences before using tunnels (n = 23, range: 1–15 d). Salamanders traveled up to 78 m along fences before successfully using tunnels (mean ± SE, 26.9 ± 4.45 m; n = 23).

Only one of nine candidate models for predicting tunnel use was supported (Table 1A). This model ($w_i = 0.95$) included the parameters distance and direction. Model-averaged parameter estimates for covariates of tunnel use, odds ratios, and confidence intervals are presented in Table 1B. Akaike-weighted odds ratios for these variables indicated that salamanders immigrating to Linnet Lake were 19.5 times more likely to use tunnels than emigrating salamanders (Table 1B). Immigrating salamanders were more likely to move longer distances along fences to reach the tunnel than were emigrating salamanders (Table 1B). The odds of successful tunnel use seem to decrease slightly with increasing body size and distance from the nearest tunnel entrance (Table 1B); however, because the 95% CI of the odds ratios for these parameters bound zero, it is impossible to conclude whether there was any real effect of these variables on probability of tunnel use.

Timing of Long-toed Salamander migrations.—The peak spring immigration period in 1994 started on 12 April, 22 days earlier than in 2008 and 21 days earlier than in 2009, when the peak immigrations began in early May. In all three years, the peak immigration period ended between 12–15 May, and thus was notably longer in 1994. The peak spring emigration period in 1994 began seven days and 19 days earlier than in 2008 and 2009, respectively. Across the three years, the peak emigration period lasted from 21 to 29 days (Fig. 2). The peak fall migration period in 2008 lasted 41 days, and occurred from 3 September to 14 October. Average snout–vent length of males and females was similar between years and migration seasons (Table 2).

Relationship between precipitation and variation in Long-toed Salamander capture rates.—The effect of precipitation (days with or without rain) on capture rates (captures/day) for emigrating and immigrating salamanders varied between years (G-test of independence, $\chi^2 = 61.8$, df = 7, $P < 0.001$). Salamander capture rates were typically higher on days with precipitation, and this relationship was stronger during emigration than immigration (G-test of interaction, $\chi^2 = 25.1$, df = 2, $P < 0.001$). An exception was observed in 2009, when the capture rate during immigration was higher on days without precipitation than on days when there was precipitation (Fig. 2). In 1994, 2008, and 2009, 75%, 63%, and 43% of all immigrating salamanders were captured on days with precipitation, respectively, whereas 99%, 95%, and 90% of all emigrating salamanders were captured on days with precipitation during the same years.

Variability in location of Long-toed Salamander overwintering sites.—Sixteen Long-toed Salamanders (six males and ten females) were captured in both 2008 and 2009. Of these, 11 were captured emigrating from the lake in spring 2009 and six were individually marked. All six of these individually marked, emigrating salamanders were initially captured immigrating to Linnet Lake in 2008 (three during the fall), and never caught again until 2009, suggesting that they had overwintered on the east side of the road, close to Linnet Lake. In addition, we captured 80 Long-toed Salamanders at pitfall traps located along fence transects immediately

Table 1. Summary of (A) Logistic Regression Models and (B) Model-averaged Coefficients (β), Standard Errors (SE), Odds Ratios and Their 95% Confidence Intervals (CI) for Variables from AIC_C Models Predicting Tunnel Use by Long-toed Salamanders Based on Pitfall Trap Captures in 2009.

(A) Models	*k*	log *L*	AICc	Δ*i* AICc	w_i	Rank
Distance[a] + Direction[b]	3	−55.43	116.95	0.00	0.95	1
Distance + Direction + Distance*Direction[c]	4	−58.84	125.84	8.89	0.01	2
SVL[d] + Direction	3	−60.07	126.24	9.29	0.01	3
Direction + Distance*Direction	3	−60.28	126.65	9.69	0.01	4
Distance + Sex[e] + Distance*Direction	4	−59.70	127.56	10.61	0.00	5
SVL + Sex + Direction	4	−59.74	127.64	10.69	0.00	6
SVL + Distance + Direction	4	−59.83	127.82	10.87	0.00	7
SVL + Distance + Sex + Direction + Distance*Direction	6	−67.15	146.64	29.69	3.39E-07	8
SVL + Distance + Sex	4	−75.30	158.75	41.80	7.93E-10	9

				95% CI	
(B) Variables	β	SE	Odds ratio	Lower	Upper
Direction	2.06	1.11	19.50	3.05	72.60
Sex	0.18	0.59	1.21	0.38	3.32
Distance*Direction	0.07	0.12	1.08	0.97	1.25
Distance	−0.11	0.11	0.90	0.76	1.04
SVL	−0.14	0.11	0.87	0.75	1.01

[a] Distance from nearest tunnel entrance (m)

[b] Immigrating to or emigrating from Linnet Lake; emigration was the reference condition

[c] Interaction between distance and direction

[d] Snout–vent length (mm)

[e] Male was the reference condition; Note: log *L* = log likelihood; Δ*i* AICc = $AIC_{c,i} - AIC_c$; w_i= Akaike weight

surrounding Linnet Lake in 2008 and 2009, 78.8% (63/80) of which were captured far from the Entrance Road along the south and east sides of the lake (K. Pagnucco, unpubl. data). These individuals were all unmarked and were never captured attempting to cross the road, indicating that they also overwintered close to Linnet Lake.

Effects of habitat characteristics on spatial variation in Long-toed Salamander captures.—Soil moisture content was highest at Tunnel 3 but was only significantly higher than moisture at Tunnel 2 ($F_{3,54} = 3.4$, $P = 0.02$; Fig. 3). Habitat surrounding the four tunnels did not differ in leaf litter depth ($F_{3,54} = 2.2$, $P = 0.10$) or canopy cover ($F_{3,54} = 1.9$, $P = 0.14$; Fig. 3).

DISCUSSION

We evaluated the effectiveness of newly installed, under-road amphibian tunnels at Linnet Lake in WLNP at mitigating road mortalities of Long-toed Salamanders. To determine how fences and tunnels interacted to direct salamanders across the road, we calculated ''fence/tunnel efficiency.'' We modeled probability of tunnel use based on salamander size, sex, direction of movement, and initial distance from tunnel entrance in order to determine if only certain individuals used tunnels. To determine the importance of precipitation during peak Long-toed Salamander migration periods, we tested for differences in Long-toed Salamander capture rates on days with or without precipitation based on migration direction and study year. To characterize movement corridors used by Long-toed Salamanders, we correlated spatial variation in tunnel use based on habitat characteristics. The strength of our between 1994 and 2008–2009 comparison would have been enhanced if additional data existed to describe historical conditions.

Drift fence/tunnel system reduced road mortality of Long-toed Salamanders.—The extensive drift fence/tunnel system built along the Entrance Road in WLNP was successful at reducing access by Long-toed Salamanders and other amphibians to the road surface, consequently reducing road mortalities to <2% of Long-toed Salamanders that attempted to cross the road in both 2008 and 2009. In contrast, a comparable study conducted at the same site in 1994, prior to the addition of drift fencing and tunnels, found that 10% of Long-toed Salamanders that attempted to cross the Entrance Road were killed by vehicles (Fukumoto, 1995). Similarly, the installation of barrier fences to guide animals to a single culvert near Lake Jackson in Florida led to a decrease in turtle road mortalities from 11.9 to 0.01 individuals/km/day (Aresco, 2005). Given the necessity of installing drift fences in combination with tunnels in order to guide animals toward tunnel entrances, it is impossible to determine whether the fences or the tunnels (or the combination of both) was responsible for the dramatic decline in road mortality seen in our study. In addition, our conclusions regarding the importance of tunnels/fences in reducing salamander road mortality would have been strengthened by the inclusion of mortality data collected from more than one pre-tunnel year to describe historical conditions.

Factors affecting tunnel use by Long-toed Salamanders.—Deployment of amphibian tunnels is a new conservation strategy in North America and Europe, and relatively few studies have documented their success. In California, only

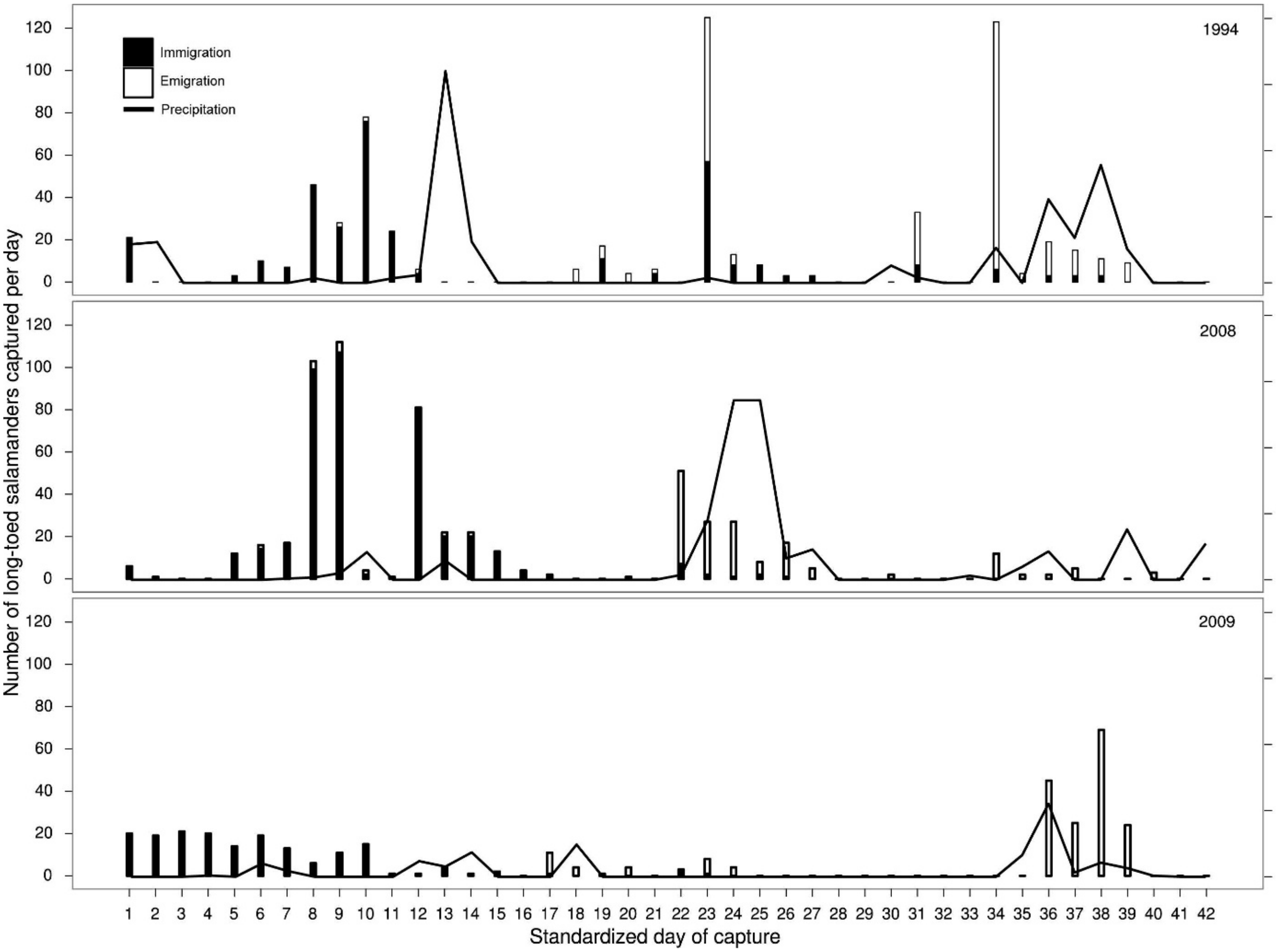

Fig. 2. Movement phenology of Long-toed Salamanders at Linnet Lake in Waterton Lakes National Park. Shown is the number of individuals captured per day during peak spring immigration (from terrestrial habitat to Linnet Lake) and emigration (from Linnet Lake to terrestrial habitat) periods in 1994, 2008, and 2009, as well as the amount of precipitation (mm) on these days. Data from 1994 were acquired from Fukumoto (1995).

9% of the endangered Santa Cruz Long-toed Salamanders (*Ambystoma macrodactylum croceum*) that encountered drift fences passed through tunnels during immigration (Allaback and Laabs, 2003), which was similar to the 12% effectiveness reported for smooth newts (*Triturus vulgaris*) in Germany (Brehm, 1989). However, tunnel effectiveness was considerably higher for a population of spotted salamanders (*Ambystoma maculatum*) in Massachusetts, where 68% of spotted salamanders captured along fences used tunnels (Jackson and Tyning, 1989). In our study, 23% of immigrating Long-toed Salamanders and 1% of emigrating salamanders that encountered drift fences were subsequently captured in exit traps after presumably moving through the tunnels. Discrepancies in tunnel effectiveness can at

Table 2. Mean (± 1 SE) Body Size (SVL in mm) and Mass (g) of Female and Male Long-toed Salamanders Captured in Pitfall Traps during Immigration to and Emigration from Linnet Lake in Spring (2008 and 2009) and Fall (2008).

Season	Year	Direction	Sex	*n*	SVL (mm)	Weight (g)
Spring	2008	Immigration	Females	203	64.3 ± 0.3	6.1 ± 0.1
			Males	196	60.9 ± 0.3	5.1 ± 0.1
		Emigration	Females	95	65.3 ± 0.5	5.6 ± 0.1
			Males	58	62.2 ± 0.4	5.0 ± 0.1
	2009	Immigration	Females	125	65.2 ± 0.4	5.5 ± 0.1
			Males	42	60.8 ± 0.6	4.4 ± 0.1
		Emigration	Females	87	64.2 ± 0.5	5.0 ± 0.1
			Males	106	61.1 ± 0.4	4.7 ± 0.1
Fall	2008	Immigration	Females	10	65.2 ± 1.0	6.2 ± 0.5
			Males	5	61.1 ± 0.8	4.9 ± 0.2
		Emigration	Females	4	64.6 ± 2.8	5.6 ± 0.6
			Males	12	62.4 ± 1.0	5.6 ± 0.3

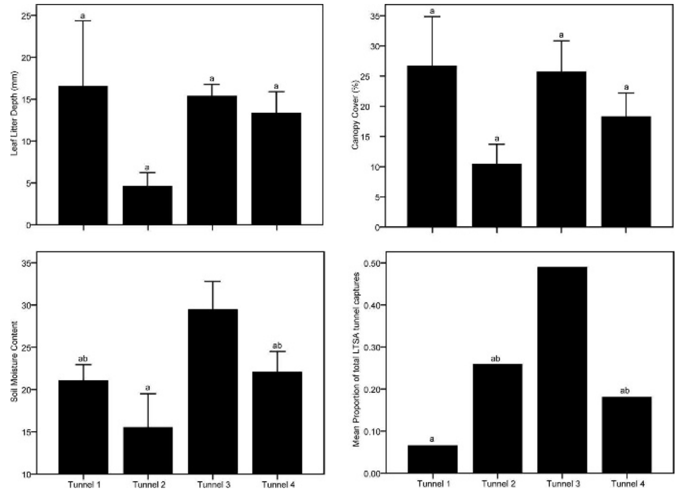

Fig. 3. Mean (±SE) leaf litter depth (mm), canopy cover (%), and soil moisture content (% saturation), as well as proportion of total Long-toed Salamanders (LTSA) captured in pitfall traps at each tunnel exit. Variables were measured every 15 m along each fence leading to each tunnel ($n = 9$ for Tunnel 1; $n = 12$ for Tunnel 2; $n = 17$ for Tunnel 3; $n = 19$ for Tunnel 4). Bars with same letter are not significantly different from one another (Tukey's HSD *post hoc* test; $P \geq 0.017$).

least partially be attributed to fence orientation; in both our study and that of Jackson and Tyning (1989), fences were angled toward tunnel entrances, whereas the fences in Allaback and Laabs (2003) were parallel to the road. Therefore, as proposed by Jackson (2003), angling fences toward entrances appears to encourage tunnel use by amphibians.

An alternative explanation for differences in tunnel effectiveness may be differences in monitoring techniques. Both Allaback and Laabs (2003) and our study used pitfall traps to monitor tunnel use, whereas Jackson and Tyning (1989) visually monitored tunnel exits for salamanders. This latter method ensures that the vast majority of salamanders using tunnels are documented. In contrast, cameras mounted in our tunnels documented 26 salamanders using tunnels that were not subsequently captured in exit traps (Pagnucco et al., 2011). These 26 salamanders represent 47% of all salamanders photographed in the tunnels and 25% of the animals captured in exit traps, suggesting low detectability based on trapping. Combining camera and tunnel exit trap data, at least 130 Long-toed Salamanders used the tunnels when migrating between overwintering and breeding habitats in 2009, which represents 10% of the total breeding population (Pagnucco et al., 2011). Considering the number of salamanders that evaded detection by either cameras or traps, our monitoring methods underestimated use of the tunnels.

The length of drift fences leading to tunnel entrances has been thought to be an important factor in determining amphibian use. For example, Allaback and Laabs (2003) did not observe any Santa Cruz Long-toed Salamanders passing through tunnels after following drift fences for more than 16 m. Although our results showed that Long-toed Salamanders traveled an average of 27 m, and up to 78 m, along fences before successfully using tunnels, our models suggest that individuals found closer to tunnel entrances were more likely to use tunnels. Thus, roadside drift fences may have been acting as a barrier to Long-toed Salamander movement. If salamanders do not access a tunnel within a short period of time, they will often return to the terrestrial habitat without breeding (Frey and Niederstrasser, 2000; Schmidt and Zumbach, 2008). In some situations, the barrier effect of fences has been found to be even more harmful to populations than the mortality caused by vehicle collisions in the absence of fencing (Jaeger and Fahrig, 2004). If the majority of salamanders are failing to reach Linnet Lake because they are being deterred by fencing, the resulting decreases in reproductive output and juvenile recruitment may be more damaging to the population than road mortalities of adults. This warrants continued monitoring of the fence/tunnel system adjacent to Linnet Lake.

Our models revealed that body size and sex did not have significant effects on probability of tunnel use by Long-toed Salamanders. This suggests that a wide range of adults are equally likely to use tunnels. The lack of effect of body size on tunnel use may partially be attributed to the fact that we only captured one juvenile and no young-of-the-year in two years of study, leading to low variability in observed salamander body sizes.

Tunnel use by Long-toed Salamanders may increase over time as salamanders adapt to the presence of these structures within their terrestrial habitat. Most Long-toed Salamanders reach sexual maturity at three years of age and have a typical lifespan of six to seven years but up to ten years in Alberta (Russell et al., 1996), suggesting that individuals have the potential to negotiate road tunnels on several occasions throughout their reproductive life. One of the major failures of short-term studies of crossing structures is that they fail to provide insights on habituation of wildlife to such large-scale landscape changes (Opdam, 1997). Individuals require time to accept crossing structures (Land and Lotz, 1996; Clevenger and Waltho, 2000; Donaldson, 2005), and habituation may take several years as individuals experience, learn, and adjust behavior (Clevenger et al., 2002). Although use of wildlife passages have been shown to increase as mammals learn a structure's location and become accustomed to it over time (Land and Lotz, 1996), such adaptive behavior has yet to be documented for amphibians.

Effects of precipitation on timing of Long-toed Salamander migrations.—Movement of Long-toed Salamanders to Linnet Lake in the spring was not strongly dependent on precipitation, which is contrary to the majority of cases reported in the literature on amphibian migrations (Semlitsch, 1985; Beneski et al., 1986; Sexton et al., 1990; Greenberg and Tanner, 2004; Todd and Winne, 2006). Although salamanders likely require moist substrates to migrate, in WLNP moisture during immigration often results from snowmelt as opposed to rainfall. Seepage from snowmelt was proposed as the catalyst for emergence from winter hibernacula for a Long-toed Salamander population in Canmore, Alberta (Sheppard, 1977). In contrast, we found that virtually all emigration later in the active season occurred on days with rain. In both 2008 and 2009, emigration at Linnet Lake began in mid-May after long dry periods (K. Pagnucco, pers. obs.), at which time any amount of precipitation appeared to trigger movement. Also, salamanders must arrive at the breeding site early enough to assure that larvae have time to metamorphose (Werner, 1986), but no such time constraint exists for emigration during the late spring; thus, precipitation should be more strongly correlated to emigration than to immigration. Additional data are required to identify

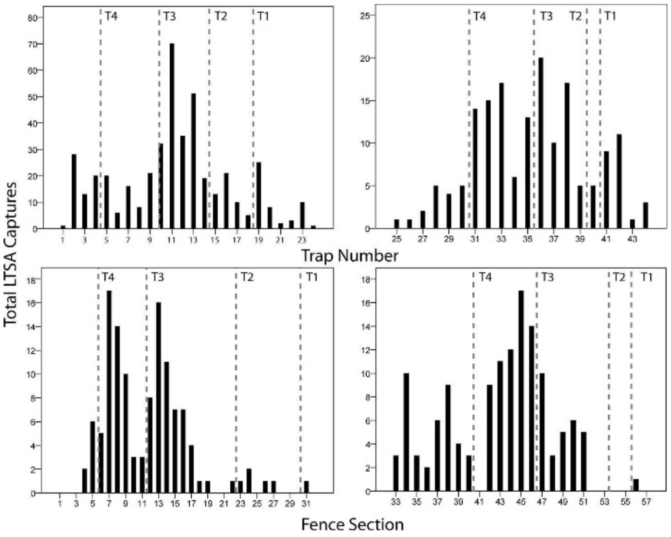

Fig. 4. Total number of Long-toed Salamanders (LTSA) captured at roadside pitfall traps during peak immigration (A) and peak emigration (B) in 2008, and along fence sections during peak immigration (C) and peak emigration (D) in 2009. Tunnel locations relative to trap and fence locations are indicated by the dashed line (T1–4 = Tunnel 1–Tunnel 4).

specific triggers of Long-toed Salamander migrations, especially during the spring.

Access of Long-toed Salamanders to overwintering habitats.—Almost 75% of all salamanders captured in tunnel exit traps were individuals immigrating to the breeding site. Our models showed that immigrating salamanders were almost 20 times more likely to use tunnels than emigrating individuals. In addition, of the 16 Long-toed Salamanders we captured in both years, 38% were individuals that we captured immigrating to Linnet Lake in 2008 and recaptured emigrating in 2009. We also captured 80 individuals around Linnet Lake, none of which were subsequently captured crossing the Entrance Road. Habitat analyses conducted in 2008 indicated that suitable overwintering habitat was common along the west, south, and east sides of the lake (K. Pagnucco, unpubl. data). These data suggest that some adult salamanders successfully overwinter in areas close to the breeding site and do not annually migrate across the road. Whether a salamander migrates or not may depend on the availability of suitable terrestrial habitat and the size of the population. If the Linnet Lake population grows and the more-favorable foraging and hibernating sites close to the lake become occupied, more salamanders may be forced to migrate further to access overwintering sites on the west side of the road. If emigrating salamanders do not use the tunnels readily and are confined to Linnet Lake, the population may decline through time as accessible terrestrial habitat becomes limited.

Effects of habitat characteristics on spatial variation in Long-toed Salamander captures.—The four tunnels were not used equally: almost 50% of all salamanders caught in tunnel exit traps used Tunnel 3 (Fig. 2). Immigration and emigration corridors used by salamanders when traveling to or from Linnet Lake were similar in 2008 and 2009 (Fig. 4). I found that the soil moisture content was highest in the habitats surrounding the entrances of Tunnel 3, which may explain higher use of this tunnel.

Data collected by Pagnucco (2010) revealed that shrub cover was an important habitat feature during salamander immigration movements at Linnet Lake, and consequently, planting shrubs adjacent to tunnel entrances may increase use. A variety of studies have shown that cover in the vicinity of passage entrances increases their use by target vertebrate species (e.g. Bennett, 1991; Rodriguez et al., 1996; Clevenger and Waltho, 2005), primarily because cover provides protection from predators.

Continued monitoring will be needed to determine if tunnel use by Long-toed Salamanders increases through time, as individuals become increasingly familiar with these new structures and tunnels accumulate organic matter, providing conditions more closely resembling natural substrates. Alternatively, substrate (e.g., fine sand or organic matter such as leaf litter, wood chips, or peat moss) and natural vegetation can be directly added to tunnel entrances, actions that have been shown to enhance the ''attractiveness'' of crossing structures and allow habitat continuity (Glista et al., 2009). Long-term monitoring is also required to determine the rate at which reductions in vehicle-caused mortality of salamanders translates into increases in population size or if the barrier effect of fences results in population declines that exceed the mortality caused by vehicles in the absence of fencing. Monitoring programs must also investigate other causal mechanisms responsible for ''natural'' population gains or losses (e.g., changes in weather patterns, water quality, land cover, levels of predation or interspecific competition) in order to assess properly the utility of under-road tunnels as a conservation tool for amphibian populations.

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